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STRUCTURE OF A PRIMITIVE NOTOUNGULATE CRANIUM[1]

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Constituting, as they did, the most abundant and varied element in the vertebrate fauna of a large continent throughout the long duration of the Tertiary, the notoungulates are of exceptional interest and importance. Adding to, rather than detracting from, this interest are their origin, the peculiarity of their structure, and the difficulty of interpreting their history. Study of the later forms, particularly those of the Santa Cruz and of the relatively impoverished Pampean, has revealed most of the surface morphology of a number of divergent lines. In the endeavor to interpret these data and to approach solutions to the many problems which arise from them, we are now turning to the oldest known forms, and especially those of the Casamayor Formation (so-called "*Notostylops* Beds"), of Eocene age.

This study of the older notoungulates embraces two points of view and bears on the study of the notoungulates in two ways. First, the early forms may be considered as the culmination of still more ancient development. They may be compared with an abstraction or hypothesis as to the generalized ancestral ungulate, subungulate, or protoungulate, and they may be compared with actual groups which developed elsewhere in the world, such as the condylarths or the hyracoids. These Casamayor notoungulates stand somewhere near a possible phyletic union with these other groups, and their study is the best approach now available for the study of the genetic origin of notoungulates and of the morphologic origin of their peculiarities. Second, these early forms may be considered as the root or base of later notoungulate development. Within the Notoungulata they can or may clarify structural problems, by showing the form in which the structural peculiarities first appeared. They should also greatly illuminate phylogenetic obscurities, not only by giving criteria for distinguishing basic ordinal characters from those progressive in or peculiar to the various phyla but also by showing these phyla at a period when they were so little divergent that

[1] Publications of the Scarritt Expeditions, No. 26.

their affinities had not yet been masked, at least to such a degree, by specialization peculiar to each line.

Peculiar interest and difficulty in this connection attach to the cranial characters. Even in the later forms some of these are not well understood and there are many points that have been, and still are, the subject of radical differences of opinion. Materials for the study of the Casamayor genera have been very inadequate, and until quite recently no detailed studies of their cranial morphology have been undertaken.

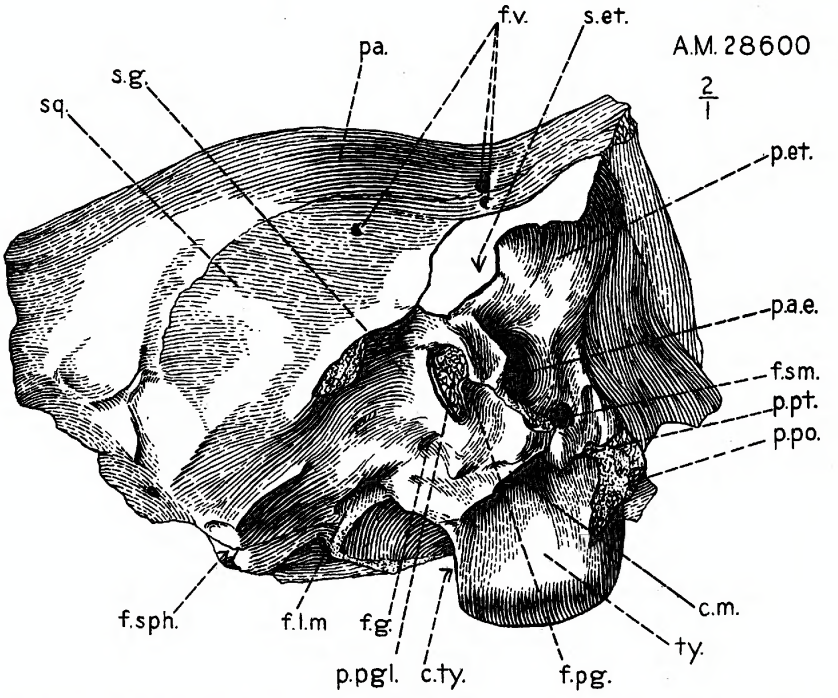

Fig. 1. *Oldfieldthomasia.* Lateral view of left half of cranium. For abbreviations see p. 29. Twice natural size.

The purpose of this paper is to describe the cranial morphology of a Casamayor notoungulate that is a rather generalized representative of its order. One specimen, incomplete in some respects and unclear in others, cannot give complete knowledge of its genus, and knowledge of one genus, primitive but certainly not generalized in every respect, cannot be completely representative of primitive notoungulate structure. Nevertheless, a useful approach toward that ideal is possible.

The specimen studied is Amer. Mus. No. 28600, an isolated but nearly complete cranial portion of a skull found by Justino Hernández in the Casamayor Formation of "Cerro Blanco,"[1] southern Chubut, Argentina. As no teeth were found with the specimen, absolutely certain identification is impossible. The genus is, however, almost surely *Oldfieldthomasia*, on this evidence: it closely resembles the skull of *Oldfieldthomasia*[2] *debilitata* in the Museo Nacional in Buenos Aires; it does not so nearly resemble known skulls of other genera; its size is appropriate for the most characteristic and common species of *Oldfieldthomasia* and less definitely within the probable range of other genera; *Oldfieldthomasia* is one of the commonest genera of this horizon; and other common genera such as *Notostylops* or *Notopithecus*, are definitely ruled out by differences in their known cranial morphology. Specific identification is impossible, but it might be of the common species *O. debilitata* or *O. furcata* (possible synonyms).

The cranium is preserved with practically no crushing, an extraordinary rarity in this formation, and the internal matrix is hard and firm, almost ideal conditions for sectioning. The condyles are missing and most of the projecting processes and crests are broken or somewhat eroded, but the more essential internal structure is well preserved. The specimen is adult or senile, with most of the sutures indistinguishable on the surface, but they are seen with much better, although not perfect, clarity in sections.

The most important part of this study is based on serial sections which were made by a simplified method described elsewhere (Amer. Mus. Novitates No. 634). Some points are left obscure, but on the whole the results are satisfactory and provide a wealth of accurate detail seldom previously equaled in the study of any fossil mammal.

The cranium was first sawed vertically along the midline. The left half was preserved for surface morphology and orientation, and the right half was embedded in plaster (hardened with gum and shellac) and sectioned serially. A series of parasagittal sections at intervals of 0.4 mm. were taken. Sectioning was begun at the most lateral point, and recording started when sufficient bone of the ear region was exposed to be in an area of distinctive preserved morphology. The sections from this point are numbered serially from 1 to 54, covering a thickness of 21.2 mm. Section 1 is 24.6 mm. from the midline of the skull, and sec-

[1] A local descriptive name, not official or distinctive. In this sparsely populated and poorly surveyed region, no very exact way of designating localities yet exists. Our Cerro Blanco is on the south rim of the Cuenca de Sarmiento, southwest of Lago Colhué-Huapí, and west of the famous barranca south of that lake. A map is in preparation.

[2] Placed in *Acoelodus* by Ameghino.

tion 54 is 3.4 mm. from the midline. Subsequent cuts revealed nothing of interest, being beyond the ear region and all foramina and in the uniform and simple basicranial axis.

The principal record is in the form of a careful camera lucida drawing, twice natural size, of each section. The drawing was carefully checked by me in each case, and the actual section also studied closely before proceeding to the next cut. This recording and the drawings here published are by Mrs. Mildred Clemans. Coleman S. Williams prepared the specimen for sectioning and rendered other assistance.

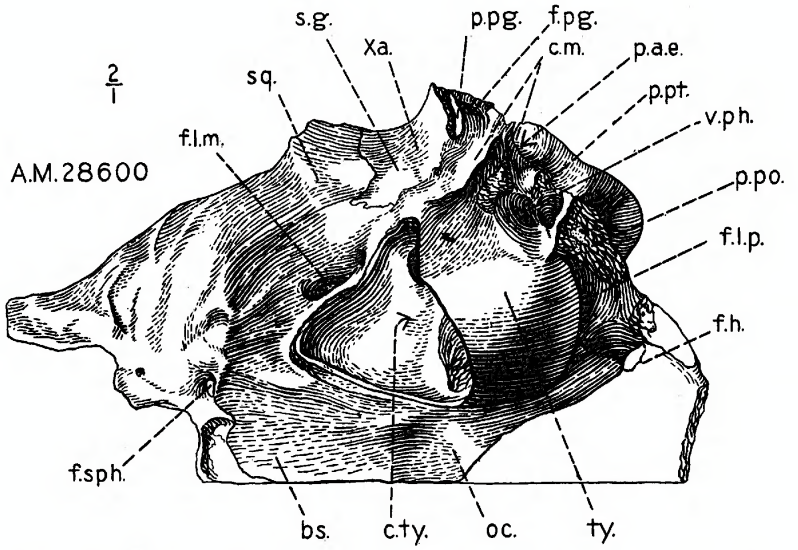

Fig. 2. *Oldfieldthomasia.* Ventral view of left half of cranium. For abbreviations see p. 29. Twice natural size.

In the study of the sections, use was also made of transparencies, both on paper and on glass, that could be superposed to show the natural relationships, and also of projections in various planes reconstructed from the sections. The external morphology of the unsectioned half was studied in the ordinary way, and also by soaking the specimen in xylol until the bone became almost transparent.[1] Many other specimens of notoungulates were also studied, but are not specifically described in the present paper. One of *Pleurostylodon* is, however, figured to assist

[1] This useful general procedure of immersion in studying fossils has previously been used to good effect by Stensiö, Noble, and others. Xylol proved particularly suitable in the present case, and has the advantage that the bone returns to its original condition when thoroughly dried.

in visualizing part of the structure of the closely similar *Oldfieldthomasia* skull.

No previous work of just this sort or in quite such detail seems to have been done on fossil mammals, but the work by Patterson on external cranial characters of notoungulates and that of Van Kampen and Van der Klaauw on the tympanic region of mammals in general (see reference at end of paper) have been particularly useful.

BONE ELEMENTS

This section is concerned with the number of individual bones present and their identity, not primarily with their topography, which is described below or adequately shown in the figures.

The only elements in the cranial roof (anterior to the supraoccipital) are the squamosal and the parietal, which are here readily distinguishable in the sections and in the unsectioned half of the skull.

The sutures in the anteroinferior region are more confusing, the sutural lines being very complex and often nearly in the plane of the sections, which greatly obscures them, but after close study, with transparencies, it appears that there are here, anterior to and above the bulla, four different elements. One is continuous with the basisphenoid medially, extends laterally below the sphenorbital fissure, forms a strip along the anterolateral edge of the bulla including the anterior rim of the foramen lacerum medium, and finally disappears in the somewhat confused region anterior to the lateral corner of the bulla. This clearly must be the alisphenoid.

A second element forms the upper rim of the sphenorbital fissure and the vertical cranial wall anterior to this and extends laterally for a short distance, about to section 40. This I take to be the orbitosphenoid. A still more anterior element, poorly developed in the sections because the anterior break barely includes its posterior end, appears anterior to and above the orbitosphenoid with a clear suture against the latter (section 45) and against the parietal (section 40) and disappears at about the same point laterally (about section 38). This is probably the posterolateral edge of the frontal.

Overlapping and, at its extreme medial end, partly inserted into the alisphenoid, first appearing definitely in about section 39 (in going through the sections from the midline outward), is another element which becomes larger laterally until it excludes the alisphenoid from contact with the parietal and in the area anterior to the glenoid surface forms the whole inferolateral wall of the cerebral cavity. With the

lateral disappearance of the parietal, the element in question is seen to be continuous with the dorsal part of the squamosal and is, of course, part of that bone.

The individuality of the periotic and its extent are not in any doubt. There are only two sections (26 and 27) in which there is any possible question as to its outline, and here only because it rapidly expands posteriorly, with the lateral boundary of this extension nearly in the plane of the section so that it is not clearly shown.

The occipital elements are completely fused with each other without

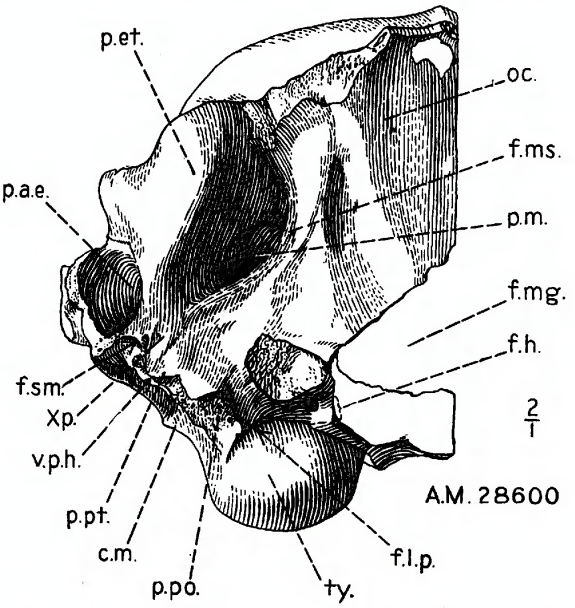

Fig. 3. *Oldfieldthomasia.* Posterior view of left half of cranium. For abbreviations see p. 29. Twice natural size.

any trace of division, so that they are simply labeled "occipital" in the sections and other figures. The only place in which this compound occipital is not clearly separated from the adjacent bones is in the median ventral axis, where the basioccipital is completely fused with the basisphenoid, although the presence of a slight ridge and the relationships to the endocranium show where this division occurred.

It is regarding the elements of the ear region that there has been the greatest question. These are very poorly understood, and unfortunately the present specimen is not sufficiently well preserved nor are its sutures

sufficiently clear at every point for a complete solution of this intricate problem. It does, however, provide many data, some of which are of particular interest and value. In order to discuss the problem, a brief historical review is necessary.

The Order Notoungulata was first defined by Roth (1903) on the structure of the ear region, which he considered unique among ungulates. An essential point was his belief that the parts usually formed by the squamosal are in notoungulates formed by a number of different elements. In the general posterolateral region he recognized the following bones as distinct:

1. *Squamosum* [the squamous part of the squamosal].
2. *Elementum zygoma* [the zygomatic process of the squamosal, said to be suturally separated in some cases].
3. *Elementum serriale*, with the *pars mastoidea* [around and above the auditory notch and containing the epitympanic sinus].
4. *Petrosum* [containing the inner ear, and also exposed on the occiput].
5. *Tympanicum* [which he said to be continuous with the *posttympanicum*].[1]

Roth homologized these with various reptilian elements in a way thoroughly discredited by later research and requiring no further discussion.

Scott (1912, p. 290), in discussing toxodonts, rejected Roth's identification of element 3 as the mastoid, and pointed out that the epitympanic sinus lies in part of the squamosal, said on Roth's authority to be sometimes suturally separate from the squamous part. This he calls the *pars serrialis*, thus giving the term a slightly different concept from that of Roth, since the latter labels with this name the supposed lateral extension, and also inferolateral into the postglenoid process, of his supposed mastoid, a possibility not discussed by Scott. Scott identified the plate between postglenoid and posttympanic processes (in *Nesodon*) as the mastoid (true mastoid, not of Roth).

Sinclair (1909, p. 71), describing the Santa Cruz typotheres, speaks of the epitympanic sinus as being in the mastoid, and figures an occiput of *Hegetotherium* in which, in addition to the occipital elements, there are suturally separate "mastoid" and "posttympanic" exposures, the names being applied as they were by Roth in this region.

Patterson (1932) differs from Scott and agrees with Roth in considering the plate between postglenoid and posttympanic processes as part of

[1] Roth's paper is very difficult to follow, as the terminology is not consistent throughout, some *lapsi* evidently occur, and the subject is inherently very complex. In spite of earnest effort, I am not certain that I have correctly grasped every detail of his apparently somewhat contradictory opinions. Patterson (1932, p. 19) evidently gathered that Roth considered the posttympanic as a separate bone, while I understand Roth to mean that it is part of the tympanic. There is also some question as to whether Roth invariably considered his "serrialis" and "mastoid" as the same bone, but apparently he did.

the tympanic. He agrees with Scott and differs from Roth and Sinclair in considering the epitympanic sinus to be in a "pars serrialis" of the squamosal. The occipital element which Roth called posttympanic and (if I rightly understand him) believed to be part of the tympanic, is stated by Patterson to be a separate entity in some but not all notoungulates. He suggests, without approving, homology with the tabular.[1] He homologizes Roth's "protuberantia petrosa" with the true mastoid.[2] Patterson later (1934) suggested that the "posttympanic" or "adventitious bone" might be part of the mastoid, but considered this as improbable.

Regarding certain of these questions the present study gives answers which, anticipating the evidence, are as follows:

1. The epitympanic sinus is not in the mastoid but in part of the squamosal.
2. The "posttemporal" or "adventitious bone" is not part of the mastoid, nor of the tympanic.
3. The plate between postglenoid and posttympanic processes is part of the tympanic.
4. The region around and above the meatus, including most of the part labeled "serrialis" by Roth, is not, as he thought, continuous with the epitympanic sinus wall (at least in this specimen).
5. Roth's "protuberantia petrosa" is the true mastoid, in as far as that element can be said to occur at all.

These conclusions refer primarily to the specimen principally studied in this paper, but from comparison with many other specimens and with the literature it seems probable that they are also valid generalizations for the Notoungulata as a whole. They are in essential agreement with Patterson's views, based on external characters of early members of all suborders. This much of the notoungulate structure now seems to be beyond probable doubt.

Turning to the details of the present specimen, the occipital sutures are very obscure, as usual, but can be almost certainly and fully determined in the sections. By a method of projection from the latter, a reconstructed posterior view of the essential portion of the occiput can be made (Fig. 4). Five suturally separate bones appear in this view:

1. The occipital (its elements completely fused).
2. The squamosal, enclosing the epitympanic sinus.

[1] No final conclusion is possible and it would be futile to discuss the matter in detail at present, but I have gone rather thoroughly into the supposed occurrence of tabulars in mammals and believe it highly unlikely that this notoungulate element, at least, can be so homologized.

[2] Which is unquestionably correct. There may, however, be a slight confusion in the criteria used to distinguish this from the "posttemporal." One cannot be categorical without study of the original specimens, but it seems very possible that the element labeled "mastoid" in certain of Patterson's figures (e. g., 3, 4a) really is, or includes, Roth's posttemporal, Patterson's adventitious bone. It is perhaps this confusion, if it exists, that led him later to suggest that the "adventitious bone" may in fact be part of the mastoid.

3. The tympanic (forming the bulla and part of the meatus, not extending onto the occiput proper).
4. The periotic, or its pars mastoidea.
5. The "adventitious bone," marked Xp.

The wall of the epitympanic sinus, although somewhat broken (especially in the lateral part), appears to be a single bone and is surely separate from any of the elements below it. There are some cracks above which may suggest, in single sections, that a suture against the squamous part of the squamosal is present, but in no case is this clearly a suture and studying the whole series of sections it seems very improbable that a suture is present at all, in this specimen. The epitympanic sinus appears to be an inflation of the squamosal, proper, well distinguished topographically but not a distinct osseous element. Roth based his belief that the epitympanic walls, and in some cases subjacent parts as well,

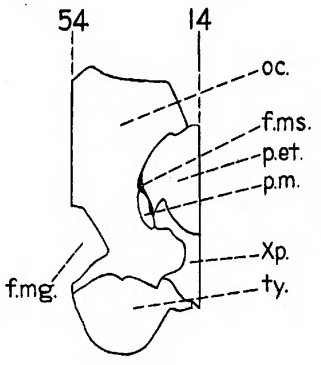

Fig. 4. *Oldfieldthomasia.* Diagram of part of right half of occiput, from sections 14 to 54, reconstructed from serial sections. For abbreviations see p. 29. Natural size.

form a separate element in notoungulates on the very rare supposed presence of a suture against the squamosal. Apparently he only believed himself actually to have observed this suture in two cases, and these are open to question, since there is a strong possibility that the supposed suture is merely a crack. As far as I know, no subsequent student has recorded a suture in this region, all (see especially Sinclair, Scott, Patterson) indicating the epitympanic wall (whatever they call it) as fused with the (rest of the) squamosal. Without denying the possibility of sutural separation, it is fair to say that none is demonstrated and the epitympanic wall may at least provisionally be considered as a part of the squamosal, for which I propose the name *pars epitympanica.*[1]

[1] This non-committal, correctly descriptive term seems very much preferable to the only really available previous designation, *pars serrialis.* The latter term is of rather anomalous etymology and not well in keeping with modern anatomical terminology, being a neo-Latin adjective formed from the proper name Serres. It implies, or demands, a homology which is very dubious, that is, with the posteroinferior center of ossification in the squamosal in man. Finally, its application to the notoungulate skull has not been perfectly clear or consistent.

The true mastoid, which is very clearly shown by the sections to have nothing to do either with the pars epitympanica of the squamosal, or the crista meati of the tympanic, or the "adventitious bone," must be represented by the posterior projection of the periotic which in this genus and many (but not all) other notoungulates has a small occipital exposure.

It is the "adventitious bone," Xp, that remains extremely dubious, not as to its individuality, which is demonstrated, but as to its identity. Although it shows some apparent tendency to fuse with the tympanic in this skull, and in others studied seems to be completely so fused (being, for instance, considered part of the tympanic by Roth, as I interpret his paper, although he certainly overlooked no possible sutures in his material), there is in several sections (e. g., 17) a clear suture which cannot possibly be a crack. Even though the suture is apparently lost by fusion in other regions, its certain presence in any part is sufficient demonstration of the separate individuality of the bones in question. Its separation from the (ex-) occipital is still more certain, as the latter simply overlies it without forming a sutural connection (e. g., section 20). Separation from the pars epitympanica is not clear in all sections, probably because of the imperfection of the specimen, but is in some (e. g., section 20), and this suture clearly developed on the occiput has been distinguished externally in a number of different genera.

The only apparent true connection of this bone is seen in sections 20–22, where it passes without a visible break into a bridge of bone above the medial end of the external auditory meatus, immediately lateral to the epitympanic recess, and is in this way united with an element developed in the postglenoid process, anterior to the tympanic. This does not necessarily prove that these are the same bone, as fusion of really separate elements in the few crucial sections could well occur, but it demands new evidence to demonstrate separability.

A remarkably anomaly, and one apparently not hitherto recorded, is the presence of another "adventitious bone," or of an anterior process of the same one, in the postglenoid process, labeled Xa in the figures. The separability of this from the tympanic is clear, a distinct suture being present throughout (e. g., section 15, 20). It is equally distinct from the pars epitympanica and the periotic, both of which are in contact with it but without even a sutural union. In its more medial part, separation from the inferolateral part of the squamosal is not clearly shown, because of cracks in this region and, doubtfully, partial fusion, but laterally it has a distinct suture against the pars glenoidea of the squamosal (e. g., section 10). In the sections this is unmistakably a true suture,

and it is, furthermore, clearly visible on the other, unsectioned, half of the skull running transversely across the glenoid surface to the squamosotympanic suture anterior to the fissura glaseri, exactly corresponding with its course as shown in the sections.

On present data it seems impossible to offer a reasonable explanation of these two adventitious bones, or two parts of one as the case may prove to be. The relationships are not perfectly clear in any described specimen, and the observation of the anterior element, or part, depends solely on this one specimen. Speculation on these grounds seems unwarranted, and the observations are merely recorded to form, it is hoped, a basis for the accumulation of essential further data.[1]

In the more lateral sections (especially 7–12) there is a bone in the base of the epitympanic sinus, above and lateral to the porus acusticus, which is consistently separate in the sections. This region is, however, badly cracked and it seems probable that the bone in question is not really a separate element. At least it should not be accepted as such without further evidence.

Lying loose and out of position in the medial part of the tympanic cavity (sections 50–53) is an auditory ossicle, probably the malleus, but the section interval is too great for useful reconstruction of its form. In sections 34–36 is another small bone in the bottom of the bulla, which may be another auditory ossicle or may be only a fragment of the broken wall of the bulla.

No other bone elements are present in the preserved part of the cranium.

EXTERNAL AUDITORY MEATUS

The roughly circular porus acusticus of this form has its upper rim nearly on a level with the glenoid surface, and from it the meatus runs forward, inward, and downward, although less oblique than in many later notoungulates. The meatus (from the point where it is completely encircled by bone) runs through eleven sections (13–23, about 4 mm.). Nearly circular at first, it becomes distinctly triangular (sections 19 seq.), with one of the three approximately equal angles downward, into the tympanic. The floor of the meatus is formed throughout

[1] Not to prejudice more definitive work, I apply no name to either part. The posterior part is the posttympanic of Roth and some others following him, but Scott apparently uses the term in a somewhat different sense. The name may become fixed in this usage if the element is a unit, since it does often or always form the true posttympanic process and is descriptively posttympanic in position, but it would seem to be inappropriate and confusing if this is part of the same bone that forms the postglenoid process. Incidentally, in the latter case the whole element would seem to correspond more nearly to the "pars serrialis" of human anatomy than does the epitympanic wall to which several workers apply this name—another reason for rejecting the name in the latter application among notoungulates.

by a thick, somewhat spongy plate of the tympanic, which also seems to form at least half of the posterior wall, and in some sections apparently most of this wall. The rest of the posterior wall, the roof, and the anterior wall are formed by the "adventitious elements," as discussed elsewhere.

The serial sections prove beyond any question that the ventral closure of the meatus is by a thickened extension of the tympanic, which everywhere separates the postglenoid and posttemporal processes. This strongly corroborates Patterson's view (1932, p. 18) that in toxodonts this plate is also part of the tympanic, not mastoid as Scott supposed. Conditions in this respect seem to be rather uniform throughout the Notoungulata, and all the specimens known to me permit the generalization that there is in this order always a tympanic plate between postglenoid and posttympanic process, the occurrence of a meatus spurius reported by Sinclair 1909 for *Protypotherium*, Scott 1912 for *Homalodotherium*, and Van Kampen 1905 for *Typotherium* is in no case substantiated and probably the report is due to failure to recognize the separate origin of a fused tympanic extension.[1]

The crista meati (Patterson 1934) is strongly developed on the present specimen and was apparently very prominent, although somewhat broken and hence not well shown in the sections. The crest is double, because of the development in it of a deep, very sharply defined longitudinal groove.[2] The posterior crest, or posterior rim of groove on the crista, abuts simply against the bulla posterior to the vagina processus hyoidei. The anterior crest swings forward on the external part of the bulla and ends internal to the glenoid fossa. Between the end of this and the postglenoid process, immediately posterior to the fissura glaseri, there is an isolated papilla of bone on the tympanic.

Upon arriving at the tympanic cavity, the internal lower rim of the meatus flairs out, becoming a semicircle of greater diameter than the meatus proper, and projects into the cavity as a pronounced crista tympanica,[3] which is open above (see section 25).

TYMPANIC CAVITY AND EPITYMPANIC SINUS

As in all notoungulates, the bulla is completely ossified, inflated, and (except, of course, for part of its dorsal wall) entirely formed by the

[1] The reported instances have all been denied by other workers. Scott seems to contradict Sinclair's statement, and Patterson's studies negative those of Scott and of Van Kampen.

[2] Possibly a canal, as a possible junction below may be broken away, but this seems improbable. Another skull of *Oldfieldthomasia* has an even larger groove, also open as preserved. Both crests are certainly on the tympanic.

[3] Note that the "tympanic crest" of Patterson's first paper (1932) is not the "crista tympanica" of other anatomists, and that he later (1934) renamed it the "crista meati."

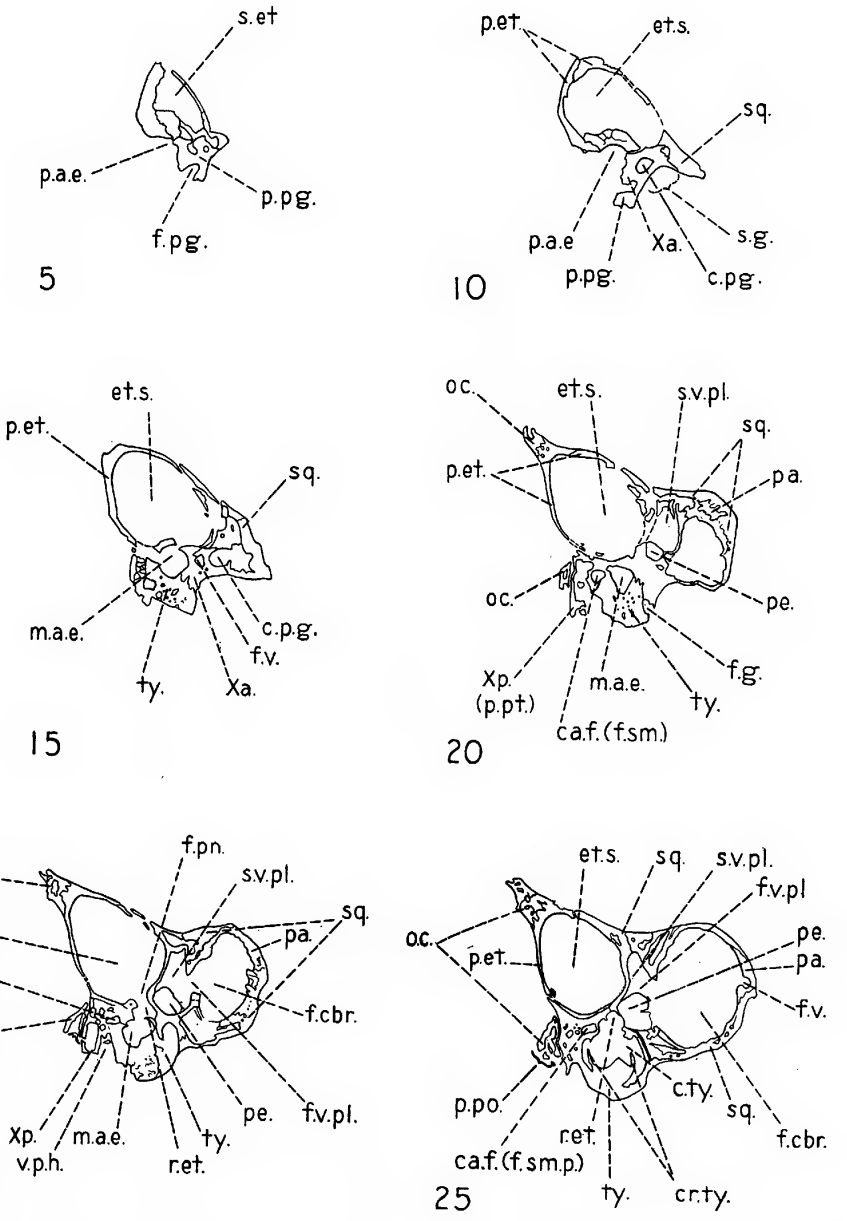

Fig. 5. *Oldfieldthomasia.* Parasagittal sections of cranium. The numbers correspond to those of the complete series of sections, see text. The right side is anterior. For abbreviations see p. 29. Natural size.

tympanic,[1] which is without any distinct trace of sutures. The recessus epitympanicus and, still more, the sinus epitympanicus are very distinct, although opening into the tympanic cavity, but the primary tympanic cavity and the hypotympanic sinus are completely hollow and poorly or not differentiated from each other. The complications in the walls of this large cavity are very few, the internal wall being for the most part a simple curved surface parallel to the visible outer surface.

There is a semicircular lateral extension of the cavity around the crista tympanica (sections 24–26). Immediately medial to this point there is a large but shallow pocket in the lateral wall at the posteroinferolateral point of the bulla (section 28) and immediately dorsal to this is a small projection, which disappears between two sections (present in 28, completely absent in 29). In section 29 a small pocket in the anterior wall of the bulla appears, and posterior to this, projecting into the tympanic cavity, are two low but definite projections. In the next section, 30, the small pocket merges into the general lumen of the bulla, and the ridge is single but with a hooked end and is considerably more prominent. Hence, in sections 31 to 33, the ridge becomes lower but stouter and more dorsal, until it reaches and passes into the dorsoanterior edge of the bulla wall. After this point the wall of the cavity is smooth and evenly curved.

Patterson has noted the presence of a septum bullae in typotheres (mentioned in Patterson 1934, but details not yet published), and it is well known that the hypotympanic sinus may be cancellous in various notoungulates. In the present skull it is not cancellous, and it seems unlikely that any real homologue of a septum bullae is present, although it is perhaps conceivable that the ridge just described is a vestige of that structure.

The tympanic gap ("tympanicumdefekt") extends to the extreme lateral edge of the cavity and indeed of the meatus, the tympanic itself not forming a closed ring until section 43. In the meatus and in small part at the beginning of the tympanic cavity the gap is apparently filled by the "adventitious elements," discussed elsewhere. In section 25 the periotic also appears in the roof of the gap which by section 28 it entirely occupies. The gap is here at its maximum. In section 33 it begins to be noticeably smaller and in 43 the edges of the tympanic meet beneath the periotic and the gap is closed, although the periotic continues to overlie the thin superior wall of the cavity nearly as far as the latter extends.

[1] I shall use "tympanic" for the entire element, without regard to a possible combination of ectotympanic and entotympanic elements.

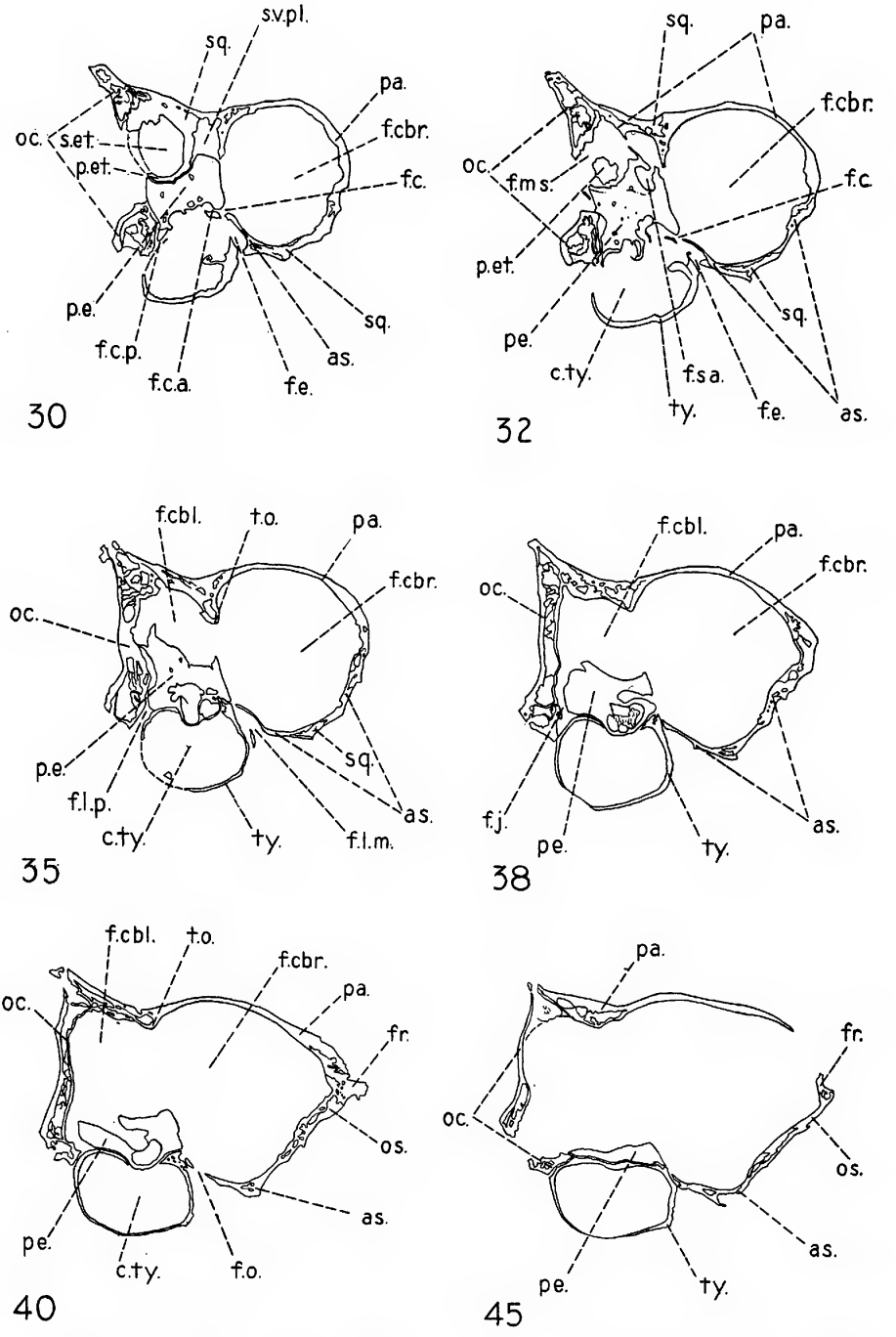

Fig. 6. *Oldfieldthomasia.* Parasagittal sections of cranium. The numbers correspond to those of the complete series of sections, see text. The right side is anterior. For abbreviations see p. 29. Natural size.

The structure of the exposure of the periotic in the tympanic cavity is discussed below.

The course of the entocarotid artery is not shown with complete clarity and while the following observations seem highly probable they are not certain. This vessel apparently enters the tympanic cavity through a very small foramen, entirely in the tympanic, opening into the fissure between the posterior edge of the bulla and the paroccipital process, immediately medial to the more produced part of the latter, and lateral to the foramen lacerum posterius, which is included in the medial extension of the same fissure. The course of the entocarotid from this point within the bulla cannot be followed, not being clearly impressed on any osseous part, but presumably it traversed the bulla around (medial

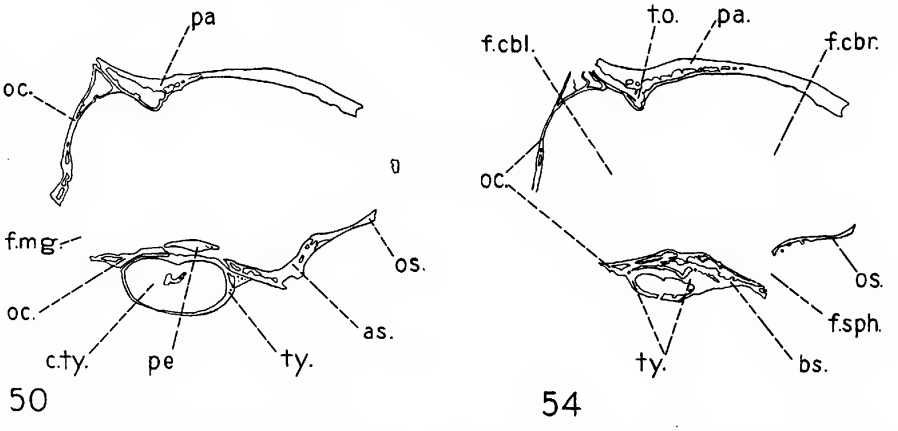

Fig. 7. *Oldfieldthomasia.* Parasagittal sections of cranium. The numbers correspond to those of the complete series of sections, see text. The right side is anterior. For abbreviations see p. 29. Natural size.

to) the promentorium. In section 31, immediately lateral to the promentorium, a groove appears below and anterior to the last trace of the latter, immediately anterior to what is rather surely the sulcus facialis, which is in all probability a sulcus caroticus, and this is seen in the same section (also in 30 to 32) to run anteriorly into a foramen. The roof, lateral wall, and floor of this foramen are formed by the periotic, the latter by a small reflected process from near the base of the processus perioticus superior. The medial wall is formed by the edge of the tympanic, which here rises to abut against the anteroinferior angle of the body of the periotic (section 33 and all medial to that). It seems sufficiently probable, although not certain, that this foramen is the foramen

caroticum anterius. Although the course of the carotid within the bulla cannot have been straight, this anterior foramen is almost exactly anterior to the probable foramen caroticum posterius, both appearing in the same section (31). It opens into the large fissure anterolateral to the bulla, above the canalis tubarius, and lateral to the foramen ovale. The artery did not course for any distance along this fissure, however, for immediately anterior to the probable foramen caroticum anterius and scarcely separated from it is a foramen between the periotic and the alisphenoid, into the posterobasal part of the cerebral fossa which must (if other indentifications here made are correct) be the (true or primary) foramen caroticum.

In any case it is certain that the entocarotid does not in this genus, as it does in *Hegetotherium* and some other notoungulates, pass between the tympanic and periotic on one side and the basioccipital and basisphenoid on the other, wholly outside the tympanic cavity.

The eustachian tube apparently left the bulla through the gap (prominent in section 30) immediately below the reflected periotic process flooring the foramen caroticum anterius, between this and the tympanic, and entered a short, oblique canalis tubarius running downward, forward, and medially, between the tympanic and the alisphenoid. This opens inferiorly along the fissure on the anterolateral edge of the bulla, posterolateral to the foramen ovale, and well removed from the anterior point of the bulla. There is no styliform process. This arrangement is apparently primitive for notoungulates, but in many later forms the tube, after emerging, channeled the outer surface of the bulla nearly or quite to its anterior end and a styliform process often developed. In some cases (possibly in *Protypotherium*, for instance) the channel may even have become a closed canal in the tympanic, but the material available to me does not absolutely prove this.

The epitympanic recess has the form of a nearly cylindrical meatus from the tympanic cavity into the epitympanic sinus. Its mouth is visible in section 25, opening in the extreme superolateral part of the cavity, above the inner end of the external auditory meatus. Thence it runs externally (in reverse order of numbering sections) and upward. Section 24 is near the outer edge of the opening into the tympanic cavity, and the inner part of the opening into the epitympanic sinus is just appearing. In 22 the canal is above the inner end of the auditory meatus, from which it is here completely separated by a bony wall, and widely open into the epitympanic sinus, appearing as a groove on the floor of the latter. This groove disappears at about section 19,

which is at the midpoint of the sinus (midpoint from side to side).

The epitympanic sinus is well developed, as it is in all notoungulates. It has approximately the size, and somewhat the shape, of the bulla, being egg-shaped, with its larger end directed downward and forward. Above the external auditory meatus the floor of the sinus, formed by the thick roof of the meatus, is bowed upward. Following the sections toward the midline, this irregularity disappears and the opening into the epitympanic recess, already described, appears. Aside from these features, the wall of the cavity is very simple and smoothly concave. The wall is somewhat cracked and broken, especially the more lateral parts, so that the absence of other openings cannot be positively affirmed, but none can be surely identified and any present must have been small and insignificant.

PERIOTIC

Almost every detail of the complex and interesting periotic bone is revealed by the serial sections of the cranium which forms the chief subject of this study, and the principle surface features are also visible in Santa Cruz specimens of *Hegetotherium* and of *Protypotherium* incidentally examined.

The outer form of the bone is very complex, but without marked differentiation into distinct elements. The central mass comprises the pars vestibularis s. canalium, which is more posteroexternal and is the principal part cut by sections 27–33, and the pars cochlearis, which is more anterointernal and forms the greater part of sections 38–42, the sections between these showing both about equally.

The posterior part of the bone is exposed over a small area on the occiput (limited by dotted lines in section 29–33). It is clear that the exposed part is practically undifferentiated from the pars canalium and represents no marked projection of the bone. Descriptively this is a pars mastoidea, very poorly developed. It is, of course, impossible to determine in a fossil whether a separate center of ossification is really represented, nor is it of any great consequence. The important points are that the mastoid region is poorly developed, uninflated, surely has nothing to do with the epitympanic sinus (not even being exposed in the floor of the latter), and develops no true processus mastoideus. These characters seem to be common to all notoungulates, as far as I can surely determine. In *Oldfieldthomasia*, at least, this small occipital exposure is the only point at which the periotic is visible externally in an undamaged skull. In other cases even this small exposure may occur in so deep

and narrow a cleft as to be practically invisible from the outside. The periotic is produced medially into a thin sharp crest loosely over-

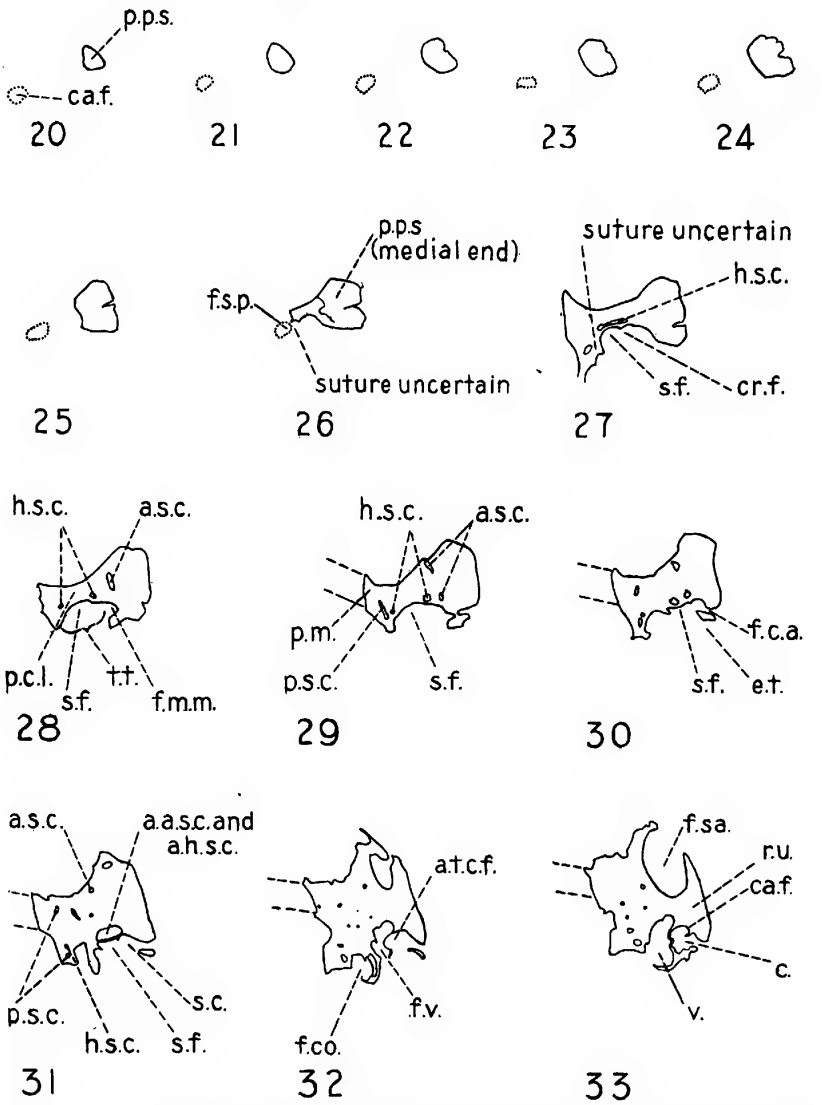

Fig. 8. *Oldfieldthomasia.* Parasagittal sections of periotic. The numbers correspond to those of the complete series of sections, see text. The right side is anterior. In sections 20 to 26 the facial canal is not in or on the periotic, but its position is shown by dots. In sections 29 to 33 the two broken lines delimit the portion of the mastoid exposed on the occiput. For abbreviations see p. 23. One and one-third times natural size.

lying the inner edge of the tympanic (the bulla), from which it departs far enough to leave a noticeable gap. The basioccipital and basisphenoid here separate and leave a gap beneath the periotic, so that although the latter tends to overlap them it is no more than barely in contact with them at any point and they do not really separate the periotic from the tympanic. The medial periotic surface above this crest is a sloping, simple surface with few features beyond the internal auditory meatus and the fossa subarcuata. The latter is broad and shallow, much less pronounced than in *Protypotherium*, for instance. The anterior surface, which abutted against the pyriform lobe of the cerebrum, is approximately triangular in plan, nearly plane, and slopes upward and backward.

The inferior, or inferolateral, surface has on its medial and posteromedial parts a large nearly smooth surface which is more or less closely applied to the corresponding part of the tympanic here roofing the bulla. Lateral to this, nearly in the middle of the inferior periotic face but nearer its anterior border, the strong, swollen promentorium appears. It is inserted in one side of the tympanic gap, and so is exposed in the tympanic cavity. On the lateral side of this appear the several openings into the middle ear, discussed below, and above these the shelflike projection of the prominentia canalis lateralis, which reaches to the edge of the epitympanic recess, and the lower surface of which forms the tegmen tympani.[1] From the anterolateral point of the main body of the periotic arises a strong, conical or styliform process, over 2 mm. in length, which extends almost straight laterally along the floor of the posterolateral cerebral venous sinus. This is at least analogous to a processus perioticus superior, and I have so designated it. Its relations are well shown in section 20, the most lateral section showing it, and in section 25, which is immediately lateral to its merging with the main body of the periotic. In the latter, the anterior face of the process shows a deep fissure, also visible in 24 and 26–28, which is not shown by the sections to be the mouth of a canal, and the function of which I do not know.

Turning to the internal structure of the periotic, the course of the facialis nerve is shown clearly. It enters, as usual, by the internal auditory meatus, where an upper groove for it is first (in proceeding from the midline) seen clearly in section 40. In 39, where the meatus is enclosed, this is a marked superoanterior pocket, and in 38 it becomes a separate canal above the cochlear cavity, into which the duct of the auditory

[1] Commonly so-called, but not entirely analogous to the part so designated in human anatomy, which is the roof of the epitympanic recess. In *Oldfieldthomasia* the periotic reaches the recess but forms no significant part of its walls, so that a tegmen tympani in the human sense is lacking.

nerve has now entered. In the same section the canalis facialis shows a branch that runs straight forward and opens into the cerebral cavity. This is clearly the hiatus canalis facialis for the nervus petrosus super-

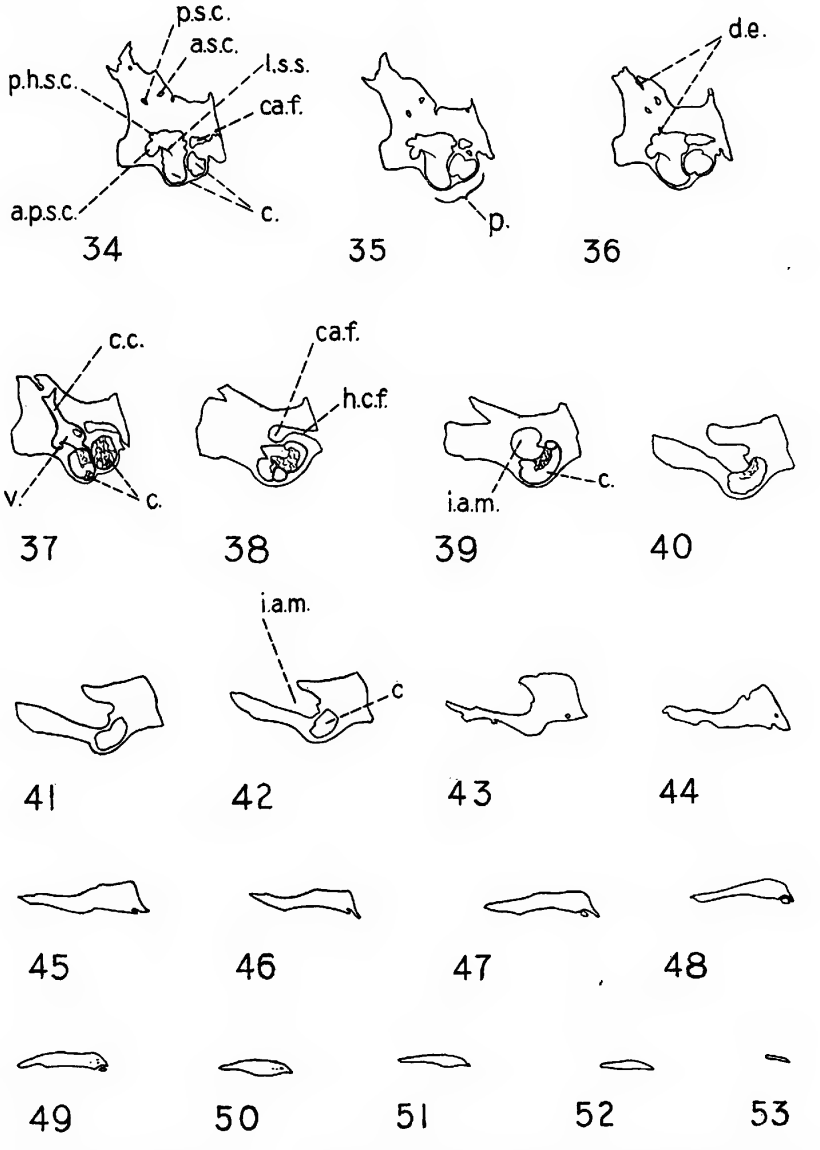

Fig. 9. *Oldfieldthomasia.* Parasagittal sections of periotic. The numbers correspond to those of the complete series of sections, see text. The right side is anterior. For abbreviations see p. 23. One and one-third times natural size.

ficialis major. The canalis facialis, proper, continues internally above the anterior part of the cochlea and anterior to the vestibule, from which it is at times separated only by a very thin film of bone, and finally in section 32 emerges into the tympanic cavity through the apertura tympanica canalis facialis, immediately anterior to the fenestra vestibuli. It crosses the roof of the tympanic cavity in a shallow open groove, running at first a little laterally, then almost straight posteriorly. Section 29 is cut almost along this part of the sulcus facialis and most of the lower margin of the periotic in this section was probably underlain by the facialis. At the edge of the periotic, in section 27, the facialis is in a more pronounced groove, and here turns and runs more externally, leaving the periotic and, section 26, entering another canal through the foramen stylomastoideum primitivum. Although now beyond the periotic, its further course may be followed. It continues in this canal, which is in the unidentified posteroinferior ?squamosal element near its suture with the tympanic, and passes laterally through the bone above and very slightly anterior to the vagina processus hyoidei. It then bends very slightly backward, and then emerges at the stylomastoid foramen, immediately below and behind the porus acusticus and lateral to the vagina processus hyoidei.

The angle between the planes of anterior and posterior semicircular canals is approximately 85°, between those of anterior and horizontal canals about 90°. The other characters of the semicircular canals are well shown in the sections, and present no notable peculiarities.

In section 36 a canal is seen to leave the superoposterior part of the vestibule, and a canal is seen (as also in 37) entering the cerebellar cavity posterior to the fossa subarcuata. The canal being of smaller diameter than the section distance, 0.4 mm., its intermediate portion is lost and was not noticed when the section was ground, but it is probable that these are the two ends of the same canal and that it is for the ductus endolymphaticus. In section 31 another extremely small canal is seen in the area between the various sections of the semicircular canals. Between 30 and 31 this was seen to continue in the direction of its long diameter in 31 and to open into the small gap between the petrosal and the wall of the epitympanic sinus, but its lower end could not be followed. Aside from a few extremely minute holes, barely visible under a binocular (e. g., in section 32), which seem merely to be slight defects in ossification or traces of cancellous structure, no other small canals were observed.

The cochlea and vestibule are well shown in the sections and seem to

present no marked peculiarities. The sections do not suffice to determine the number of turns of the cochlea, but apparently there were few, perhaps less than two, although a skull of *Hegetotherium*, broken so that the cochlea lies partly open, apparently has $2^1/_2$ turns, as in most ungulates. The fenestra vestibuli and f. cochleae are not very clear, since their rims are nearly in the plane of the section and the bone is very thin, but by superposing the sections as transparencies their character can be made out. The fenestra vestibuli is smaller than the fenestra cochleae and is elongate in an anteroinferior-posterosuperior direction, while the fenestra cochleae is more nearly circular although slightly elongate in the same direction. They are separated by a thin bridge of bone. In one section (32) the fenestra cochleae, fenestra vestibuli, and apertura tympanica canalis facialis may be seen arranged in a row from posteroinferior to anterosuperior, in the order named, separated by thin bony plates, appearing here as grooves since their lips are more medial.

The fossa muscularis major, for the tensor tympani, is well defined and easily recognizable, particularly in section 28, as a pocket, extending forward and upward, lateral to the apertura tympanica canalis facialis and internal to the epitympanic recess. It lies immediately above the posterior end of the canalis tubarius, from which it is, however, quite separate, and immediately lateral to and slightly above the (probable) foramen caroticum anterius.

The last named foramen, described in dealing with the bulla, is the only other important structure involving the periotic.

ABBREVIATIONS ON PERIOTIC SECTIONS

a.a.s.c., ampulla of anterior semicircular canal.
a.h.s.c., ampulla of horizontal semicircular canal.
a.p.s.c., ampulla of posterior semicircular canal.
a.s.c., anterior semicircular canal.
a.t.c.f., apertura tympanica canalis facialis.
c., cochlea.
ca. f., canalis facialis.
c.c., crus commune.
cr. f., crista facialis.
d.e., ductus endolymphaticus(?).
e.t., eustachian tube.
f.c.a., foramen caroticum anterius.
f.co., fenestra cochlearis.
f.m.m., fossa muscularis major.
f. sa., fossa subarcuata.
f.s.p., foramen stylomastoideum primitivum.
f.v., fenestra vestibuli.

h.c.f., hiatus canalis facialis.
h.s.c., horizontal semicircular canal.
i.a.m., internal auditory meatus.
l.s.s., lamina spiralis ossea.
p., promentorium.
p.c.l., prominentia canalis lateralis.
p.h.s.c., posterior opening of horizontal semicircular canal.
p.m., pars mastoidea.
p.p.s., processus perioticus superior.
p.s.c., posterior semicircular canal.
r.u., recessus utriculi.
s.c., sulcus caroticus.
s.f., sulcus facialis.
t.t., tegmen tympani.
v., vestibule.

EXTERNAL FORAMINA

The *optic foramen* is not preserved in this specimen.

The *sphenorbital foramen* is more on the inferior than on the lateral side of the cranium and is unusually close to the anterior margin of the bulla, although this may be accentuated to a small degree by breakage of the foramen wall.

A rather large, elongate fissure at about the middle of the anterolateral border of the bulla, and hence distinctly external in position represents the *foramen lacerum medium*. As shown by the internal structure, its more anteromedian end is the foramen ovale, its more posterolateral the eustachian foramen, and above the latter is the true carotid foramen which, however, does not appear at all externally.

There are no foramina at the anterior or posteromedian ends of the bulla or along its median border.

A distinct but small and irregular *fissura glaseri* is visible medial to the glenoid surface, anterior to the crista meati, at the external angle of the bulla.

The sections show that there are several postglenoid canals, but their external relationships are obscured by breakage. All are analogous in structure and function. The opening of the largest, which is the (or the principal) *postglenoid foramen* is between the glenoid surface and the porus acusticus externus, appearing as a vertical channel between postglenoid process and crista meati before it turns and runs into the bone in an anteromedian direction.

The *porus acusticus externus* is described in connection with the auditory chambers.

The *stylomastoid foramen*, which is directed laterally rather than in-

feriorly, is immediately posteroinferior to the porus, from which it is separated by a bony wall, and directly above and lateral to the vagina processus hyoidei.

The *vagina processus hyoidei* (which, of course, is not properly a foramen, having an unperforated roof) is a relatively large and deep pit in the usual notoungulate position, that is, at the posterolateral angle of the bulla. Its anteromedian wall is formed by the bulla, anterolateral by the inner end of the posterior crest of the crista meati, posterolateral by a small bridge of bone joining the crista meati and posttympanic process below the stylomastoid foramen, and posteromedian by the external part of the paroccipital process. On the unsectioned half of the skull there is a circular opening at the posterior edge of the vagina processus hyoidei which appears to be a foramen, but from the sections it appears without much doubt that this is merely a break exposing the cancelli of the adjacent bone.

A deep, narrow, vaguely double fissure on the posterior border of the bulla, between the latter and the median part of the paroccipital process, is the *foramen lacerum posterius*, which, like the f. l. medium, is thus displaced laterally with respect to the more usual position. The more lateral part of the fissure was apparently entered by the entocarotid and contains, on its anterior wall and scarcely visible externally, the foramen caroticum posterius, while the more median and more open part is the foramen jugulare.

The *hypoglossal* (or *condylar*) *foramen* is broken away on the sectioned half, and only partly preserved on the unsectioned portion. On the latter it may, however, be seen that it was relatively large, freely exposed, and approximately circular. Its opening forms a pit immediately posterior to the most posterior (posteromedian) point of the bulla, whence the canal runs upward, backward, and medially. There is a small circular opening on the anterior wall of the pit which may, however, be an artifact.

The margins of the *foramen magnum* are broken. In another specimen of *Oldfieldthomasia* it is preserved, but presents no marked peculiarities, being a simple transverse ellipse with a large, rounded basal notch.

A small opening which may be at least descriptively accepted as a *mastoid foramen*, is left by the incomplete filling of the gap on the occiput of the pars mastoidea. This opens into a channel posteromedian to the epitympanic sinus and above the pars mastoidea, opening into the posterolateral part of the cerebellar fossa.

There are several small and variable *venous foramina* on the roof of

the skull in the squamosal and parietal near their suture with each other, and at least one in the anterolateral cerebral wall.

POSTGLENOID, POSTTYMPANIC, AND PAROCCIPITAL PROCESSES

These processes are very incomplete on both sides of the sectioned skull, but are fairly well shown by another skull of the same genus.

The postglenoid process is large and prominent, compressed anteroposteriorly. Its lateral end passes into a ridge which runs upward and then curves backward, forming a semicircular eminence anterior and superior to the porus acusticus. The median end abuts against the middle of the anterolateral side of the meatus, being separated from the crista meati by a notch, which continues posteriorly and then superiorly as the groove running into the postglenoid foramen.

A posttympanic process is usually present as a morphological element in notoungulates, being a downward projection of the squamosal or of the "posterior adventitious bone," but in most cases it is applied to the side of the paroccipital process and is not topographically separate from the latter. In *Oldfieldthomasia*, however, or at least in skull Amer. Mus. No. 28896, it has a distinct apex, lateral to the paroccipital process and much less prominent than the latter. The paroccipital process, formed entirely by the exoccipital, is very prominent, directed straight downward, and apparently was simply styliform (the end is broken on all available specimens). In any case it clearly had no striking specialization such as, for instance, that of *Pachyrukhos*.

ENDOCRANIUM

I have elsewhere (Simpson 1932) described an imperfect natural braincast of *Oldfieldthomasia* which showed the more essential dorsal features of the cerebrum and olfactory bulbs. The present specimen adds nothing to knowledge of the various sulci and convolutions, the direction and thickness of the sections not being suitable for this purpose, but it clearly shows the positions of all the cranial nerves save I and II, the general proportions of the postolfactory parts of the brain, and some other details.

The general plan is clearly identical with that of *Notostylops* (Simpson 1933A), the differences being slight and of degree only. The indicated braincast might be summed up as intermediate between *Notostylops*, more primitive in this respect, and *Hegetotherium* (Simpson 1933B), more advanced, but nearer the former.

The pyriform lobes were somewhat deeper and less expanded pos-

teriorly than in *Notostylops*, but had not or had not so markedly expanded inferoanteriorly as in *Hegetotherium*. The dorsal gap between cerebrum and cerebellum prominent in *Notostylops* does not exist in *Oldfieldthomasia* (see section 54, where the crested tentorium sharply divides the two fossas dorsally), but the dorsal part of the cerebellum is still fully exposed and on a level with the cerebrum, not depressed below and partly overlapped by the cerebrum as in *Hegetotherium*. The endocranial foramina are almost exactly as in *Notostylops*, except that the internal ends of the foramina lacera anterius and medium were somewhat nearer to each other and that of the hypoglossal is not shown to be (but may nevertheless have been) double.

In the vicinity of the fossa of sylvius a small canal, evidently vascular, leaves the endocranial cavity, runs for some distance anteromedially in the bone, and then opens on the outer surface. It may be seen, near its internal origin, in section 35, and its anterior opening is in section 41. This is probably the homologue of the large anterior cerebral vessels of *Rhyphodon*, and although variable, one or more such vessels seem to be the rule in notoungulates as they are seen in almost all the skulls, well preserved in this region, that I have examined.

Special interest attaches to the posterolateral cerebral venous openings which I have previously shown (1933A, B) to be characteristic of notoungulates, although apparently not invariable as they were not detected in *Rhyphodon*. They are very well developed in *Oldfieldthomasia*, and their structure is fully shown by the sections.

In section 32, where there is still a large lumen in the cerebral region (chiefly the pyriform lobe), the cerebellar fossa, proper, is ending and the first small slice of the medial wall of the epitympanic sinus appears in its place. In the anterosuperior part of the periotic is an embayment which represents the fossa subarcuata. Above this is a space which represents an anterolateral continuation of the cerebellar cavity, and is here nearly cut off from the cerebral cavity. Laterally, in reverse order through sections 31 to 27, this continues as a large sinus, quadrate in section, bounded anteriorly by a lateral continuation of the tentorium, ventrally by the periotic, posteriorly by the wall of the epitympanic sinus, and dorsally by the skull roof (here squamosal). Its roof contains several foramina which communicate with the internal vessels and diploe of the skull roof. At least one canal (sections 26–24) also runs from outside the skull roof, through the latter along the squamoso-parietal suture, and into the sinus. In sections 26 to 23, the anteroventral part of the sinus is widely open into the cerebral cavity, here cut in its extreme postero-

lateral part. This is clearly the prominent foramen that I have described in several related genera from its trace on the braincast. External to this, the sinus becomes an encircled pocket of irregular oval shape, with the processus perioticus superior inserted in its floor and finally, about section 15, narrows and becomes a large canal which passes out laterally above the glenoid fossa, then turns downward and backward and emerges in the postglenoid foramen. There are also in this lateral region, poorly preserved in this specimen, several other smaller vascular canals, one or more of which also communicate with this sinus, which is connected with a general postglenoid venous drainage.[1]

NOTE ON A SPECIMEN OF *PLEUROSTYLODON*

Patterson has described the external features of the ear region of *Pleurostylodon* in a paper in press, of which he kindly gave me a duplicate manuscript. Another specimen of this genus, Amer. Mus. No. 28878, is broken in this region, but the parts present are unusually well preserved and show some of the external characters even more clearly than

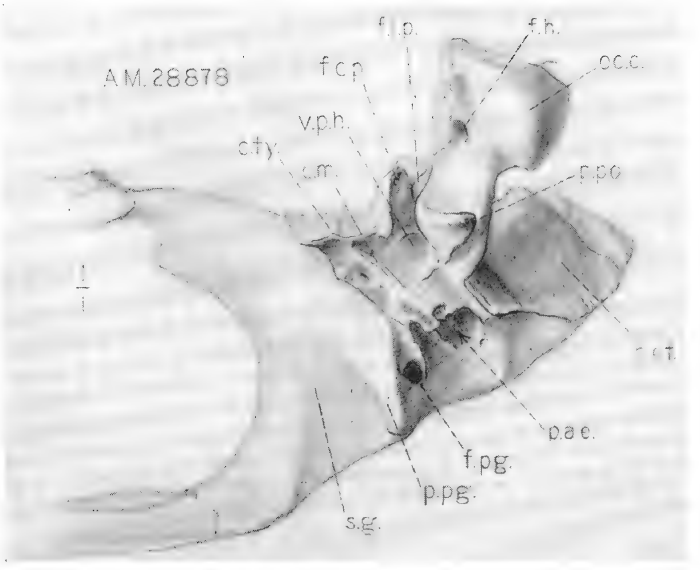

Fig. 10. *Pleurostylodon.* Ventral view of part of right half of cranium. For abbreviations see p. 29. Natural size.

[1] The canals in this region are extremely variable in notoungulates both individually and in the various groups. In *Rhyphodon*, in which the sinus is probably absent and certainly very poorly developed, I cannot detect any postglenoid foramen. In an unidentified (but surely notoungulate) skull fragment from the Deseado beds there are at least five postglenoid foramina, all uniting eventually in the sinus. In most forms there is one, usually prominent.

does Patterson's specimen, while the very fact and nature of the breakage reveal some important internal structures. Although irregular, the fracture is essentially an oblique superolateral-inferomedial section and reveals the inner faces of the outer walls of the epitympanic sinus, upper part of the tympanic cavity, foramen magnum, and posterolateral part of

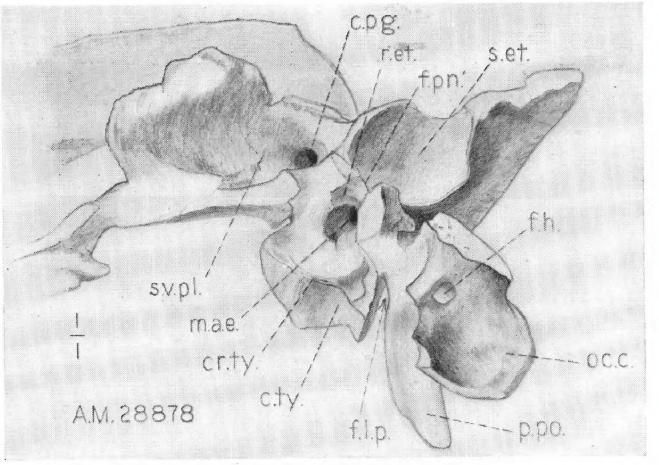

Fig. 11. *Pleurostylodon.* Medial aspect of the external part of the right side of the cranium. For abbreviations see text, below. Natural size.

the cerebral cavity. The figures are self-explanatory, in conjunction with the preceding description of the same parts in *Oldfieldthomasia*, which is closely similar in this region and the description and sections of which are, I believe, clarified and made easier to follow by the present figures.

ABBREVIATIONS ON FIGURES

(Abbreviations on the sections of the periotic, alone, are given separately on a previous page.)

as., alisphenoid.
bs., basisphenoid.
ca.f., canalis facialis.
c.m., crista meati.
c.pg., postglenoid canal.
cr. ty., crista tympanica.
c.ty., tympanic cavity.
f.c., carotid foramen.
f.c.a., foramen caroticum anterius.
f.cbl., cerebellar fossa.
f.cbr., cerebral fossa.

f.c.p., foramen caroticum posterius.
f.e., eustachian foramen and canal.
f.g., fissura glaseri.
f.h., hypoglossal foramen.
f.j., foramen jugulare, and canal.
f.l.m., foramen lacerum medium.
f.l.p., foramen lacerum posterius.
f.mg., foramen magnum.
f.ms., mastoid foramen.
f.o., foramen ovale.
f.pg., postglenoid foramen.
f.pn., foramen pneumaticum (of epitympanic sinus).
fr., frontal.
f. sa., fossa subarcuata.
f.sm., stylomastoid foramen.
f.sm.p., foramen stylomastoideum primitivum.
f.sph., sphenorbital foramen.
f.v., venous foramina and canals, not especially named.
f.v.pl., posterolateral cerebral venous foramen.
m.a.e., external auditory meatus.
oc., occipital (all elements, fused).
oc.c., occipital condyle.
os., orbitosphenoid.
pa., parietal.
p.a.e., porus acusticus externus.
pe., periotic.
p.et., pars epitympanica (of squamosal).
p.m., pars mastoidea (of periotic).
p.pg., postglenoid process.
p.po., paroccipital process (broken base in figures of *Oldfieldthomasia*).
p.pt., posttympanic process (broken base in figures of *Oldfieldthomasia*).
r.et., epitympanic recess.
s.et., epitympanic sinus.
s.g., glenoid surface.
sq., squamosal.
s.v.pl., posterolateral venous sinus.
t.o., tentorium osseum.
ty., tympanic (including entotympanic, if any).
v.p.h., vagina processus hyoidei.
Xa., "anterior adventitious element."
Xp., "posterior adventitious element."

REFERENCES

KAMPEN, P. N. VAN. 1905. 'Die Tympanalgegend des Säugetierschädels.' Morph. Jahrb., XXXIV, pp. 321–722.

KLAAUW, C. J. VAN DER. 1931. 'The auditory bulla in some fossil mammals with a general introduction to this region of the skull.' Bull. Amer. Mus. Nat. Hist., LXII, pp. 1–352.

PATTERSON, B. 1932. 'The auditory region of the Toxodontia.' Field Mus. Nat. Hist., Pub. 305, Geol. Ser., VI, No. 1, pp. 1–27.

1934. 'The auditory region of an Upper Pliocene typotherid.' Geol. Ser. Field Mus. Nat. Hist., VI, No. 5, pp. 83–89.

ROTH, S. 1903. 'Los ungulados sudamericanos.' An. Mus. La Plata, Sec. Paleont., V, pp. 1–36.

SCOTT, W. B. 1912. 'Mammalia of the Santa Cruz Beds. Part II. Toxodonta.' Rept. Princeton Univ. Exped. Patagonia, VI, pp. 111–238.

SIMPSON, G. G. 1932. 'Skulls and brains of some mammals from the *Notostylops* Beds of Patagonia.' Amer. Mus. Novitates, No. 578, pp. 1–11.

1933A. 'Braincasts of *Phenacodus*, *Notostylops*, and *Rhyphodon*.' Amer. Mus. Novitates, No. 622, pp. 1–19.

1933B. 'Braincasts of two typotheres and a litoptern.' Amer. Mus. Novitates, No. 629, pp. 1–18.

SINCLAIR, W. J. 1909. 'Typotheria of the Santa Cruz beds.' Rept. Princeton Univ. Exp. Patagonia, VI, Pt. I, pp. 1–110.